佐賀医科大学一般教育紀要
第3号（1985）P.37－53

An ESS Model for Optimal Copulation Time

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An ESS Model is formulated and analyzed to obtain the optimal copulation time for males when they compete for females. In stationary states, the optimal copulation time is shown to be a function only of the operational sex ratio (OSR) and the fertilization curve as a function of copulation time, independent of the guarding time and the searching efficiency. OSR as defined here, is the number of males in a mating site divided by the influx rate of females there.

INTRODUCTION

Mating behaviors of insects have been actively studied recently (1),(2). The main force of such activity was to introduce a theory of adaptive strategies: organisms have evolved to maximize their individual fitnesses by natural selection. For males to gain more fitness, they should locate more females and fertilize more eggs which the found females possess.

In most insects, the sperm injected by a male are alive long enough to fertilize all eggs produced by a female in her life. Therefore, when two or more males copulate with the same female, there occurs competition among their sperm for fertilization of her eggs.

In some species, it is known that males displace the

sperm which other males injected before (3),(4). Parker and Stuart (5) made a model to analyze the optimal copulation time required to maximize the total number of eggs fertilized by a male. The following is a brief review of their study.

A fresh cowpad in a meadow is soon invaded by a swarm of dungflies. The first flies to arrive are males; the females (most of them are non-virgins) start to arrive a few minutes later and they are captured by males as soon as they arrive on or near the pad. Immediately after copulation the females lay their eggs on the pad while the male guards the female from other males. The percentage of the fertilization by the male was experimentally obtained as a function of the copulation time : a longer copulation time yields the higher proportion of the fertilized eggs but the lower gradient (Figure 1).

The dungfly's dilemma of how long to spend copulating can be solved graphically. Consider a male which has just finished copulating with a female. Before he can copulate with a new female, he must first guard his present female until she has laid all her eggs. Only then can he fly off to search for a new female.

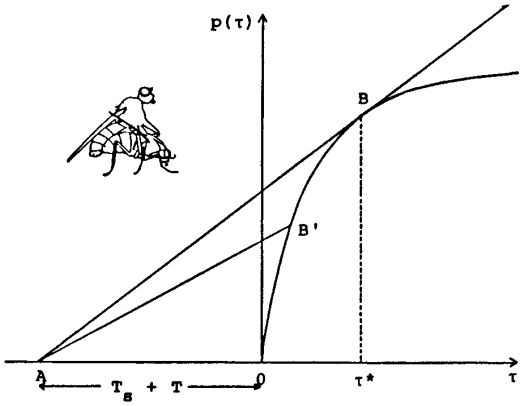

Figure 1. The fertilization curve $p(\tau)$ as a function of the copulation time τ. AO is the searching time T_s plus the guarding time T. By drawing a tangent line from A to the curve, the optimal copulation time τ^* can be obtained.

The optimal copulating time to maximize the eggs fertilized per unit time is given by drawing a tangent line from point A of Figure 1 to the fertilization curve. Parker and Stuart showed that the value thus predicted is fairly close to the observed value in the field.

In their model, however, they treated the searching time as a given parameter. This is not a good assumption in the case where there are a number of males on the pad. The changes in the copulation time of males affect the number of the actually searching males, and thus affect the searching time before a male captures a new female.

The situation given above is essentially that which holds in game theory. We shall present below a simple ESS (evolutionarily stable strategy (6)) model. Our alternative is not so much for the sake of improvement of the original model for the dungfly as it is an attempt at a basic model for the optimal copulation time which is applicable for general cases where male competition is essential.

The ESS copulation time is the strategy such that when most males adopt that copulation time, a few mutant males, which take any other copulation time, can not get more efficiency in fertilization of eggs. The dependency of parameters of the model (the operational sex ratio, the searching efficiency and the guarding time) on the optimal strategy is the central issue in the present study.

THE MODEL

Consider a mating site where a constant number of males, M, wait for females, and mature non-virgin females come in at a constant rate, f, as shown in Figure 2.

We assume that the encounter between males and females is random so that the encounter rate is $\lambda M_s F$, where M_s is the number of males actually searching, F the number of free female before copulating, and λ the searching efficiency,

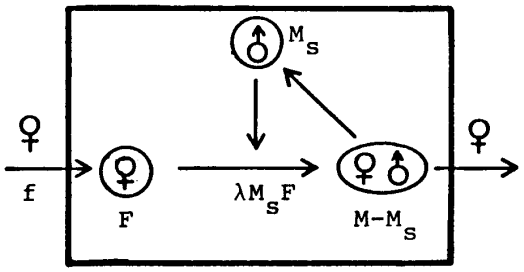

Figure 2. M males wait for females coming in at a rate f. The capture rate is $\lambda M_s F$, where M_s represents the number of searching males, F free females, and λ the searching efficiency. After copulating and guarding, each male starts to search for a new female.

dependent on the searching ability of males and the visibility of the site.

When a male finds a free female, he copulates with her for a time period, τ, in order to displace the sperm injected by other males. The proportion of the eggs fertilized by his sperm is a function of the copulation time, which is assumed to be represented by $p(\tau)$ as shown in Figure 1.

The function, $p(\tau)$, is naturally defined to be smooth, monotone increasing from 0 to 1, and concave, namely

$$p(0) = 0,\ p'(\tau) > 0,\ p''(\tau) < 0 \quad \text{and} \quad \lim_{\tau \to \infty} p(\tau) = 1 \qquad (1)$$

After copulating, for a time period, T, the male guards the female from other males until the female completes her ovipositing. Then, the female leaves the mating site, and the male starts to search for a new female.

The fitness of each male can be calculated as the rate of fertilization: the proportion of eggs fertilized by his sperm divided by the sum of the searching time, T_s, the copulation time, τ, and the guarding time, T, namely,

$$W(\tau) = \frac{p(\tau)}{T_s + \tau + T} \qquad (2)$$

Among the parameters, the copulation time, τ, is the

only strategy in which each male can make a choice. It should be noted that T_s is not constant but dependent on the strategies of other males, which will be shown in detail later.

In the first step to obtain an ESS, we assume that all males, M, adopt the same strategy, τ^*. Then, the changes in the number of free females, F(t), and the number of searching males, $M_s(t)$, can be represented, respectively, by

$$\frac{dF(t)}{dt} = f - \lambda M_s(t) F(t) \tag{3}$$

and

$$M_s(t) = M - \int_{t-(\tau^*+T)}^{t} \lambda M_s(t') F(t') dt' \tag{4}$$

Equation (3) means that the change in F(t) is equal to the influx rate minus the capture rate by searching males. The integral in Equation (4) represents the number of males which are copulating or guarding at time t; the number is equal to the number of females captured during the time interval from $t-(\tau^*+T)$ to t. Equation (4) is thus trivial: the number of searching males is equal to the total number of males minus the number of copulating or guarding males.

When the system (3) and (4) reaches a stationary state, that is, when F(t) and $M_s(t)$ approach constant values, F^* and M_s^*, respectively, after a certain time, the stationary values should satisfy the following equations:

$$0 = f - \lambda M_s^* F^* \tag{5}$$

and

$$M_s^* = M - \lambda M_s^* F^* (\tau^*+T) \tag{6}$$

and thus we have

$$M_s^* = M - f(\tau^*+T) \tag{7}$$

and

$$F^* = \frac{f}{\lambda\{M-f(\tau^*+T)\}} \tag{8}$$

As M_s^* and F^* must be positive, a necessary condition for the existence of a stationary state is

$$\tau^* < M/f - T \tag{9}$$

We can show that this inequality is the necessary and sufficient condition for the system (3) and (4) to approach the stationary state (7) and (8) when $M_s(0)=M$ and $F(t)=0$ for $-(\tau^*+T) \leqq t \leqq 0$ (see Appendix). In the case where $\tau^* > M/f-T$, $F(t)$ increases to infinity and $M_s(t)$ decreases to 0. Examples of both cases are shown in Figure 3.

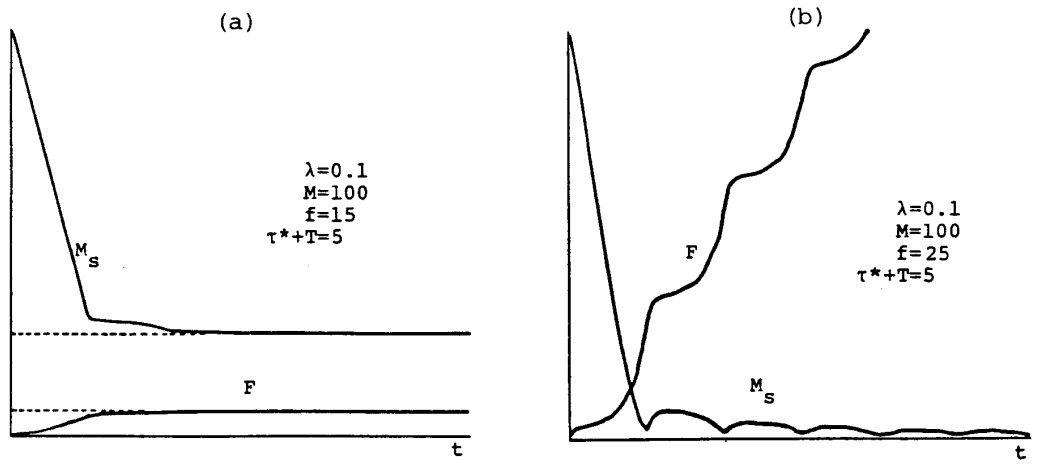

Figure 3. The changes in numbers of searching males M_s and free females F. (a) When $\tau^* < M/f-T$, F and M_s approach to stationary values. (b) When $\tau^* > M/f-T$, F increases to infinity and M_s decreases to 0. The values of parameters used for numerical calculation are shown in the figure.

In the stationary state of (7) and (8), M_s^* is a decreasing function of τ^*, and F^* is an increasing function

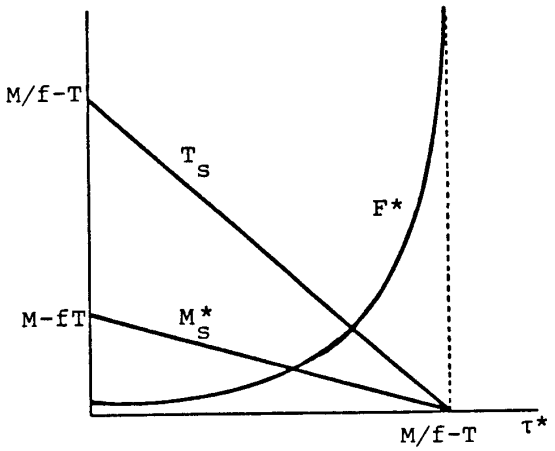

Figure 4. The stationary values F* and M_s^*, and the searchng time T_s as a function of the copulation time τ*.

of τ*, as shown in Figure 4. That is, the longer copulation time results in fewer searching males and more free females. The searching time for a male to capture a female is the inverse of the capture rate per male, namely,

$$T_s = \frac{1}{\lambda F^*} = M/f-(\tau^*+T) \qquad (10)$$

Thus, the searching time, T_s, is a decreasing function of τ* (Figure 4).

From Equations (7) and (10), we have

$$T_s = M_s^*/f \qquad (11)$$

This equation is intuitively realized because it is the inverse of the influx rate of females per searching male.

An ESS τ* is here defined as a strategy such that when adopted by most males, a small number of males adopting any other τ cannot gain higher values of the fitness in Equation (2), namely,

$$W(\tau) < W(\tau^*) \qquad (12)$$

Here, we assume that the number of mutants is so small that the value of T_s in Equation (10) can be substituted for the present case.

The technique to arrive at the ESS τ* is the same as that by Parker and Stuart (5) except for the fact that the searching time is a function of τ* (Figure 1). If

τ^* is an ESS, the line from point A (AO is T_s+T) to point B(τ^*,$p(\tau^*)$) on the fertilization curve has a maximum slope of any line AB', where B' is an arbitrary point on the curve $p(\tau)$. This means that AB is the tangent at B on the curve; we assumed that $p(\tau)$ is a smooth function.

Mathematically, the above condition is represented as

$$p'(\tau^*) = \frac{p(\tau^*)}{T_s+\tau^*+T} \tag{13}$$

Inserting Equation (10) into (13), we have

$$\frac{p(\tau^*)}{p'(\tau^*)} = M/f = s \tag{14}$$

Here, we define M/f=s as the operational sex ratio (OSR).

If a function, $p(\tau)$, is given, we can obtain the ESS $\tau^*(s)$ as a function of s. From Equation (14) and p(0)=0, we have

$$\tau^*(0) = 0 \tag{15}$$

Differentiating both sides of (14) by τ^*,

$$\frac{ds}{d\tau^*} = \frac{p'(\tau^*)^2 - p(\tau^*)p''(\tau^*)}{p'(\tau^*)^2} \tag{16}$$

and then,

$$\frac{d\tau^*}{ds} = \frac{1}{1 - p(\tau^*)p''(\tau^*)/p'(\tau^*)^2} \tag{17}$$

From Equations (1) and (17), we have

$$\tau^{*\prime}(s) = 1 \quad \text{at} \quad s = 0$$
$$0 < \tau^{*\prime}(s) < 1 \quad \text{for} \quad s > 0 \qquad (18)$$

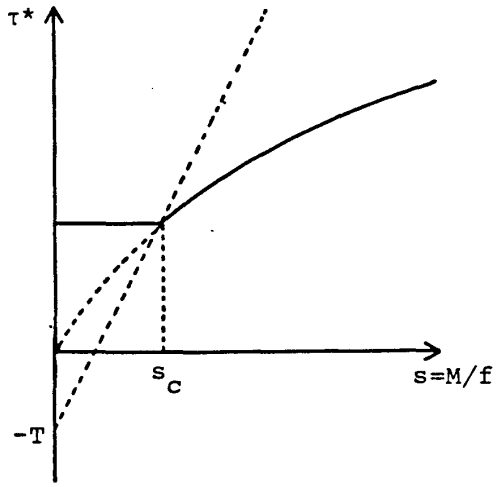

Figure 5. The optimal copulation time, τ^*, as a function of the operational sex ratio, s. The curve is a solution of Equation (14) and the line passing (0,-T) is Equation (19). The value of s at the crossing point, s_c, separates two regions. When $s < s_c$, τ^* is constant and when $s > s_c$, τ^* is a monotone increasing function of s.

Equations (15) and (18) mean that $\tau^*(s)$ is monotone increasing from 0 and has a maximum gradient 1 at s=0, as shown in Figure 5.

In order for the value of τ^* to be a true ESS, the value should satisfy Inequality (9) because we have assumed a stationary state. The boundary of this condition,

$$\tau^* = s - T \qquad (19)$$

is a straight line with a gradient 1 passing (0,-T) in Figure 5, and it crosses the curve $\tau^*(s)$ only once because $\tau^*(s)$ is a monotone increasing function with a maximum gradient 1 at origin. We define the value of s at the crossing point by s_c, and when $s > s_c$, value τ^* satisfies the stationary condition (9).

In very special cases, $\tau^{*\prime}(s) \to 1$, when $p''(\tau^*)/p'(\tau^*)^2 \to 0$ as $\tau^* \to \infty$, and it is conceivable that there are no crossing points. In such cases, we shall regard s_c as infinity in the following.

Especially when T=0, the ESS value of τ^*always satisfies the stationary state condition.

When $s < s_c$, Inequality (9) breaks down and F(t) increases to infinity. In this case, the searching time T_s

becomes 0 and the optimal copulation time can be obtained by maximizing

$$W(\tau) = \frac{p(\tau)}{\tau + T} \tag{20}$$

In this case, the situation is not game theory, but rather a simple optimization problem. Then, the ESS τ^* satisfies

$$\frac{p(\tau^*)}{p'(\tau^*)} = \tau^* + T \tag{21}$$

As this equation can be led by eliminating s from Equations (14) and (19), the value of τ^* corresponds to $\tau^*(s_c)$.

Putting together both cases, we can conclude the result of our model as follows.

When a fertilization curve $p(\tau)$ satisfying Equation (1) is given, there exists a critical operational sex ratio, s_c, dependent on T, and the value s_c separates (i)cases where competition among males is not relevant and (ii)cases where the competition is essential :

(i) If $0 < s < s_c$, the ESS τ^* is not dependent on the operational sex ratio s=M/f, but dependent on the guarding time T. Then, the number of free females, F, approaches infinity and the number of searching males, M_s approaches 0.

(ii) If $s > s_c$, the ESS τ^* is not dependent on T and the searching efficiency λ, but a monotone increasing function of the OSR, s. Then, F and M_s approach positive constant values.

In the case of the stationary state, (ii), without the mathematical analysis one might not expect that the ESS copulation time is independent of the guarding time and the searching efficiency.

We present here one example which gives an explicit solution of τ^* in the case (ii). Let the form of the fertilization curve be

$$p(\tau) = 1 - \exp(-\tau/T_c) \tag{22}$$

where T_c represents a relaxation time of saturation to 1. Then, all Equations (1) are satisfied, and from Equation (14), we have

$$\tau^* = T_c \log(1+s/T_c) \tag{23}$$

DISCUSSION

We have presented a basic model in order to formulate the situation where competition among males is essential and to get a rough idea about the dependency of the ESS on several parameters which seem to be important.

We hope that this model will be modified to apply for various actual cases. Here, we only show possible directions for improvement of several artifacts in our model.

We assumed that incoming females (non-virgins) do not oviposit before they are captured by a male for copulation. As a result, the females before copulating on the patch increase to infinity when the influx rate is very large compared with the number of males.

If the uncopulating females start oviposition with a certain probability, the changes in the free females can be represented as

$$\frac{dF(t)}{dt} = f - \gamma F(t) - \lambda M_s(t) F(t) \tag{24}$$

instead of Equation (3). Then, F(t) can not increase above the value f/γ; F(t) probably approaches a stationary value. In this case, one could easily expect that the result is almost the same as in the previous model when γ is sufficiently small compared with f and λ. When the values of γ, f and λ are comparable, the ESS value of τ^* will also be dependent on γ and λ.

The assumption of constancy in the guarding time may be unreasonable because absence of guarding will be more advantageous when the number of uncopulating females is large. However, a male should need a minimum handling time for each female before or/and after copulating. We can regard this minimum time as T instead of the guarding time.

In general, there is a problem of how long males guard a female after copulating. We shall present an ESS model of the optimal guarding time in another paper.

The incoming females were assumed to be all non-virgins. If they consist of both virgins and non-virgins, then there are two cases depending on whether or not males can discriminate between the two groups.

If they cannot discriminate, the basic model still holds good when $p(\tau)$ is regarded as the average fertilization curve of virgins and non-virgins. If they can descriminate, then different copulation times, τ_v and τ_n, respectively for virgins and non-virgins, should be spent. Thus, the ESS τ_v^* and τ_n^* must satisfy

$$W(\tau_v, \tau_n | \tau_v^*, \tau_n^*) < W(\tau_v^*, \tau_n^* | \tau_v^*, \tau_n^*) \qquad (25)$$

where $W(\tau_v, \tau_n | \tau_v^*, \tau_n^*)$ is the average fertilization rate of a mutant with a strategy set (τ_n, τ_v) when almost all males

adopt the strategy set (τ_n^*, τ_v^*). This type of extension of the model also holds for cases where females have different numbers of eggs.

Males also may be different in their abilities such as the searching efficiency, the guarding time and the fertilization curve. Then, comparison among the same type of males can help derive the ESS condition. That is, for each type of males, i,

$$W_i(\tau_i | \{\tau_j^*\}) < W_i(\tau_i^* | \{\tau_j^*\}) \qquad (26)$$

where $W_i(\tau_i | \{\tau_j^*\})$ means the fertilization rate of a mutant male of the i-th type when most males of each j-th type adopt the strategy τ_j^*.

Equations (25) and (26) represent the conditional ESS (7) where there is phenotypic variance among individuals. Whether or not clear-cut results of any use can be obtained by following such an analysis naturally remains to be seen.

Finally, we should like to take note of the generality in application that our model affords us. Thus, we can treat the problem of the optimal time investment (8) when a number of competitors search for resources which are continuously supplied and whose value is reduced through utilization. The resources may be females, food, hosts or habitats.

ACKNOWLEDGMENTS

The authors wish to thank Prof. K. Tokaichi and Prof. G. Groff, Saga Medical School for refining the English of the manuscript.

This work was supported in part by a Grant-in-Aid for Special Project Research on Biological Aspects of Opimal Strategy and Social Stracture from the Japan Ministry of Education, Science and Culture.

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APPENDIX

We put $\tau^*+T=u$ in Equation (4) in the following. Integrating both sides of Equation (3) in an interval $(t-u,t)$,

$$F(t) - F(t-u) = f \min(t,u) - \lambda \int_{t-u}^{t} M_s(t')F(t')dt' \qquad (A1)$$

where $\min(t,u)$ represents a minimum of t and u. Thus,

Equation (4) is transformed to

$$M_s(t) = M - f \min(t,u) + F(t) - F(t-u) \qquad (A2)$$

Inserting this equation into Equation (3), we have

$$\frac{dF(t)}{dt} = f - \lambda(M - f \min(t,u) + F(t) - F(t-u))F(t) \qquad (A3)$$

The solution of this equation, $F(t)$, is obviously continuous and smooth for $t > 0$.

When $M > fu$, we first show that the solution with an initial condition, $F(t)=0$ for $-u \leqq t \leqq 0$, is bounded between 0 and F^* in Equation (8).

Let t_o be the positive minimum time at which $F(t_o)=0$. Then, $F'(t_o)=f>0$, which contradicts with smoothness of $F(t)$. Thus, $F(t) > 0$ for $t > 0$.

Let t^* be the minimum positive time at which $F(t^*)=F^*$. Then, from Equations (A3) and (8), we have

$$\frac{dF(t^*)}{dt} = -\lambda(fu - f \min(t,u) + F(t^*) - F(t^*-u))F(t^*) \qquad (A4)$$

Because the right hand side of this equation is negative, $F(t)$ cannot increase above F^*.

Next, we separate the time axis into intervals

$$I_i = [(i-1)u, iu] \qquad (i=1,2,\ldots) \qquad (A5)$$

and we put

$$m_i = \min_{t \in I_i} F(t) \qquad (A6)$$

We can show m_i is a monotone increasing series for $i > 1$.

If we put t_i at which $F(t)$ has a minimum in each I_i, then there are three cases: (i) $t_i=(i-1)u$, (ii) $(i-1)u<t_i<iu$ and (iii) $t_i=iu$. In case (i), clearly $m_{i-1}\leqq m_i$. Reforming (A3) with Equation (8) for $t>d$ and putting $t=t_i$, we have

$$F(t_i)-F(t_i-u) = \frac{-F'(t_i)+\lambda(M-fu)(F^*-F(t_i))}{F(t_i)} \tag{A7}$$

In cases of (ii) and (iii), $F'(t_i)\leqq 0$, and as $F^*>F(t_i)$, Equation (A7) means $F(t_i-u)<F(t_i)$. By definition,

$$m_{i-1}\leqq F(t_i-u), \quad m_i=F(t_i) \tag{A8}$$

and therefore, $m_{i-1}<m_i$. As m_i has proved to be monotone increasing and bounded by F^*, it should approach a constant and $F'(t_i)\to 0$.

From Equations (A7) and (A8), we have

$$0 < (M-fu)(F^*-m_i) < (m_i-m_{i-1})m_i + F'(t_i) \tag{A9}$$

When t is sufficiently large, $F'(t_i)\to 0$ and $m_i-m_{i-1}\to 0$ because of convergence of $\{m_i\}$. Thus, Equation (A9) implies that $m_i=F(t_i)$ approaches F^* as $i\to\infty$.

Thus, we can conclude that $F(t)$ approaches F^*, and therefore, $M_s(t)$ approaches to M_s^* in Equation (7).

Next, we consider the case of $M<fu$. Because $M_s(t)$ in Equation (A2) is always positive,

$$F(t)-F(t-u) > -(M-fu) > 0 \tag{A10}$$

for $t>u$. This means $F(t)\to\infty$ as $t\to\infty$. In this case, $M_s(t)$

should approach to 0. Otherwise, the right hand side of Equation (A1) would approach to $-\infty$, which contradicts $F(t)-F(t-u) > 0$.

最適交尾時間のESSモデル

山村則男
辻宣行

オスがメスの獲得をめぐって競争しているとき，最適交尾時間を求めるためにESSモデルを定式化し解析した。定常状態においては，最適交尾時間は、性比と，受精率の関数形のみに依存し，ガード時間および探索効率には依存しない．ここでいう性比とは，交配場所におけるオスの数を，単位時間当たりにそこへ入ってくるメスの数で割ったものである。